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# Arthropod Phoresy Involving Pseudoscorpions in the Past and Present

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**Abstract** Pseudoscorpions form phoretic associations with a wide range of arthropods, including at least 44 families of insects and three families of arachnids. The present work brings up to date phoretic associations between pseudoscorpions and different arthropods and discusses the long-standing controversy over whether this behavior is basically a predatory response or adapted solely for dispersal. That phoresy in pseudoscorpions is of long standing and obligatory in many cases is demonstrated by its continuance for millions of years, as shown by the fossil record. A member of the Chthoniidae attached to a moth in Baltic amber is reported for the first time.

## Introduction

Pseudoscorpions have the ability to attach themselves to a variety of arthropods, mostly adult stages, which are generally more mobile. The principal benefit of this phoresy is to reach a new habitat with a potentially adequate supply of food. In this way, the distribution of the pseudoscorpions is increased and they are able to exploit transitory habitats that otherwise would be unavailable.

When such phoretic behavior originated is unknown. Although the fossil record of pseudoscorpions extends back to the Middle Devonian, some 380 million years ago (Shear *et al.* 1989), evidence of phoresy between pseudoscorpions and arthropods only appears some 40 million years ago, in the early Tertiary. The present work summarizes knowledge on extant and extinct phoretic relationships between pseudoscorpions and arthropods, discusses the controversy as to whether phoresy is predatory response or an adaptation solely for dispersal, and compares extinct with extant phoretic relationships in regards to the concept of behavioral fixity.

This review recognizes only two of Beier's (1948) three categories of associations between pseudoscorpions and arthropods as providing definite evidence of phoresis. These are when pseudoscorpions are found actually holding the appendages of carriers or when they are riding on the bodies of large arthropods. The third category, pseudoscorpions found in the nests of social insects, while suggestive of phoresy, is considered too vague to be included. However, a new category is introduced here — pseudoscorpions taken from aerial traps on ships and airplanes, indicating phoresy via a winged insect.

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An attempt is made to cite the original reference to specific examples of phoresy in various geographical areas. Extensive use has been made of previous lists of extant phoretic associations between pseudoscorpions and carriers, especially those of Vachon (1940), Beier (1948), and Muchmore (1971). Multiple references to many of the rider-carrier associations can be found in the above-mentioned works. The present list treats these associations under the carrier arthropod. Terminology follows Beier (1963) and Muchmore (1971).

## Results

Fossil records of arthropod phoresy with pseudoscorpions are limited to examples in Baltic and Dominican ambers (Table 1). Baltic amber is approximately 40 million years old and Dominican amber about 20–40 million years old, although the exact dating of the latter deposits is still controversial (Poinar 1992). A new fossil relationship reported here is a member of the family Chthoniidae attached to the abdominal tergites of a moth in Baltic amber (Fig. 1). The most commonly encountered fossil phoretic associations are between platypodid beetles and pseudoscorpions in Dominican amber (Fig. 2). Extant phoretic associations between pseudoscorpions and arthropods are presented in Table 2.

## Discussion and Conclusions

Direct evidence is provided of four families of pseudoscorpions exhibiting phoretic behavior with eight families of insects in the fossil record and ten families of pseudoscorpions demonstrating phoresy with at least 44 families of insects and three families of arachnids at present. These records will certainly increase as more fossil and recent material is examined.

In the fossil case reported here involving a moth carrying a member of the genus *Chthonius* C. L. Koch (Chthoniidae) in Baltic amber, the pseudoscorpion appears probably to be a juvenile. According to Kaestner (1970) juveniles are never involved in extant phoretic relationships. This agrees with the observations of Zeh and Zeh (1992d), who reported that with *Cordylochernes scorpioides* and the harlequin beetle, "pseudoscorpion presence on beetles is strictly an adult phenomenon". However it appears that juveniles can be phoretic in certain instances, since Sankey (1949) reported two juveniles of *Lamprochernes nodosus* riding on a *Nelima* harvestman, Jones (1978) recorded two nymphs of *Lamprochernes nodosus* attached to *Nelima sylvatica*, and Guilmette *et al.* (1970) reported a pseudoscorpion that was later determined to be a cheliferid protonymph (Harvey 1986) apparently phoretic on a fly in California.

There are two principal methods in which pseudoscorpions can make contact with their carriers in phoretic associations. The most common is when the pseudoscorpion lives in the same habitat as the carrier and makes contact when the latter has completed its development and is ready to leave the old habitat. The less common situation is when the pseudoscorpion waits for a carrier that periodically visits the habitat, such as a bee visiting flowers or collecting resin from a plant (Beier 1948, Muchmore 1971).

Legg (1975) suggested that the reason pseudoscorpions of certain families partake in phoresy more often than those in other families may be associated with the development of a complex mating behavior and the presence of spermathecae for sperm storage.

Table 1. Examples from the fossil record of arthropod phoresy involving pseudoscorpions (D=Dominican amber; B=Baltic amber). Families of pseudoscorpion genera listed: Chthoniidae (*Chthonius*), Cheliferidae (*Dichela, Pycnochelifer*), Chernetidae (*Oligochernes*), and Withiidae (*Parawithius*).

| Carrier | Pseudoscorpion | Amber type | References |
|---|---|---|---|
| | **INSECTA** | | |
| COLEOPTERA | | | |
| Platypodidae | | | |
| *Cenocephalus rhinoceroides* | *Parawithius* sp. | D | Schlee (1980); Schawaller (1981); Poinar (1992) |
| DIPTERA | | | |
| Rachiceridae | | | |
| *Chrysothemis speciosa* | Unknown | B | Ross (1997) |
| Tipulidae | | | |
| Unknown | Chernetidae | B | Schlee & Glochner (1978) |
| TRICHOPTERA | | | |
| Unknown | *Dichela berendtii* Menge | B | Beier (1948) |
| LEPIDOPTERA | | | |
| Unknown | *Chthonius* sp. | B | PRESENT STUDY |
| HYMENOPTERA | | | |
| Apidae | | | |
| *Proplebeia dominicana* | Unknown | D | Wu (1996) |
| Braconidae | | | |
| Unknown | *Oligochernes bachofeni* Beier | B | Beier (1937) |
| Unknown | *Pycnochelifer kleemanni* (C. L. Koch et Berendt) | B | Beier (1937) |
| Ichneumonidae | | | |
| Unknown | *Dichela berendtii* Menge | B | Menge (1855) |

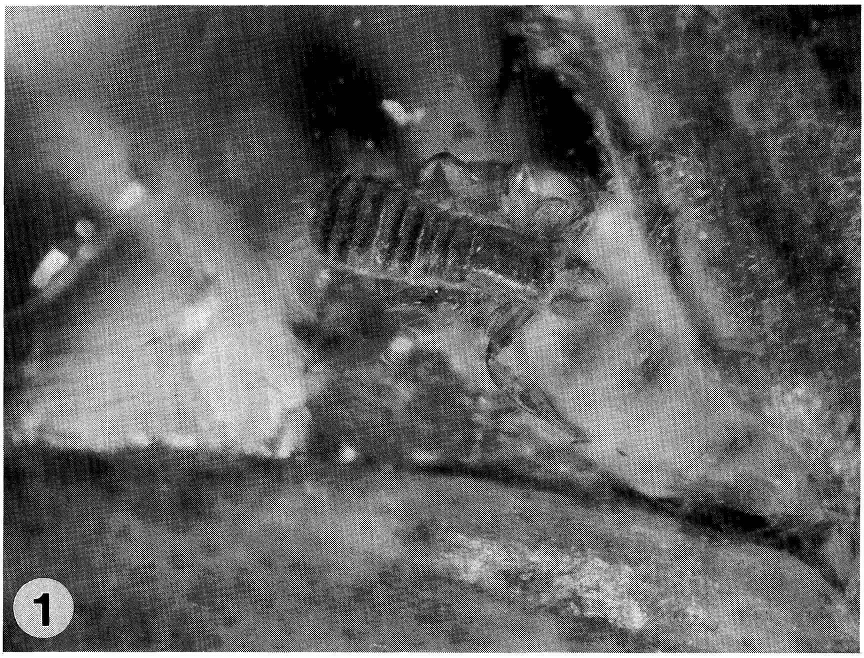

Fig. 1. A member of the Chthoniidae (*Chthonius* sp.) on the back of a moth (Lepidoptera) in Baltic amber.

These adaptations have then freed such pseudoscorpions from a purely static existence in permanent habitats and allowed them to visit temporary habitats via phoresy. Legg reasoned that this is why members of the families Chernetidae and Cheliferidae have such a wide distribution.

The carriers can range greatly in size. Some are hardly larger than the pseudoscorpion, while others dwarf the rider. Some large carriers supply not only transportation, but also a survival habitat for the pseudoscorpion; in such cases, the pseudoscorpion may have an extended association with the carrier. An example is the association between pseudoscorpions and the harlequin beetle, *Acrocinus longimanus* (Coleoptera: Cerambycidae). The pseudoscorpions live under the elytra or on other parts of the beetle, often with mites that occur in the same habitat. In the case of *Cordylochernes scorpiodes*, one of the six species of pseudoscorpions showing phoretic behavior with this beetle, males use the dorsum of the beetle as a mating site, waiting for new females to climb aboard and occasionally nourishing themselves on some of the associated mites in between periods of mating (Zeh & Zeh 1992d). In the case of these mating males, the acquisition of this habitat may be more for mating than for riding to new sites, and the back of the beetle may be the preferred habitat until that particular male is dislodged by another. That such associations are long-termed is shown by the silken security webs that are produced by the pseudoscorpions on the back of the beetle. The phenomenon of pseudoscorpions spinning silken webs on the back of harlequin beetles was first noted over 80 years ago (Calvert & Calvert 1917) and commented upon more recently (Zeh &

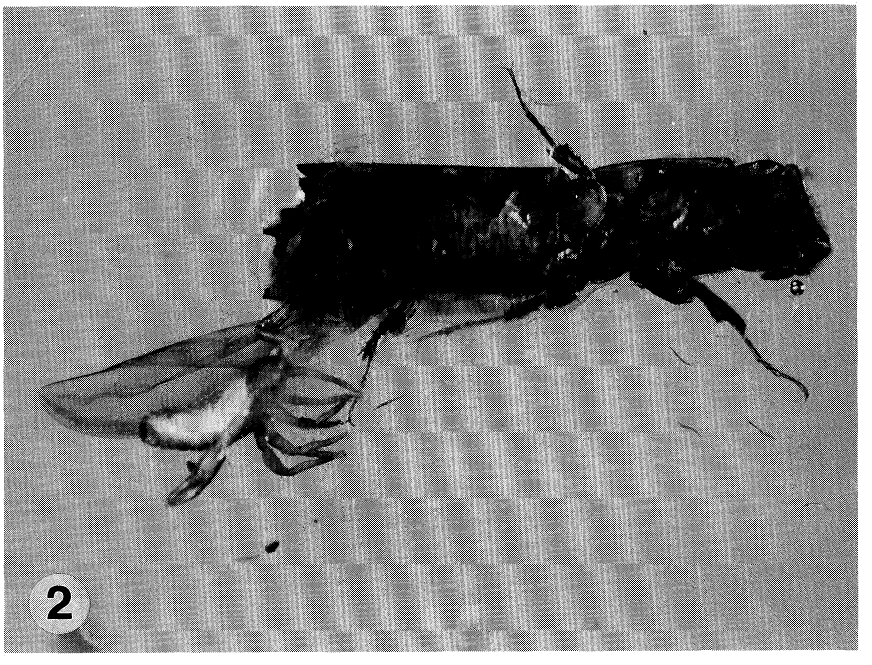


Fig. 2. An adult *Parawithius* sp. (Withiidae) holding a platypodid beetle (*Cenocephalus rhinoceroides*) (Platypodidae: Coleoptera) in Dominican amber. The location by which the rider grasps the carrier (under the posterior portion of the elytra) is similar to that reported in extant associations (see illustration in Aguiar *et al.* 1992).

Zeh 1991).

This raises the issue of phoretic pseudoscorpions feeding while riding on their carriers. Consuming mites has been documented with *Cordylochernes scorpiodes* on the harlequin beetle (Zeh & Zeh 1991) and could well occur on larger carriers where the pseudoscorpion assumes a natural position without its chela clasped to an appendages of the carrier. Pseudoscorpions carried by mammals apparently dine on microarthropods, especially mites, in the pelage of their carriers (Muchmore 1971, Durden 1991). It is interesting that some pseudoscorpions found in mammal nests which use the mammal as a carrier are themselves carriers of phoretic mites (Durden 1991). The presence of phoretic mites on pseudoscorpions carried by arthropods also occurs. One example involved uropodid nymphs on *Titanatemnus congicus*, which in turn was phoretic under the elytra of an *Acanthophorus* sp. (Cerambycidae) in the Belgian Congo (Vachon 1950). Other examples exist, but are not included in the present work.

Vachon (1940) concluded that phoretic behavior in pseudoscorpions was accidental and motivated by a predatory response (hunger for the carrier). Although Muchmore (1971) felt that the reason pseudoscorpions evolved phoretic behavior was unknown, he concluded that it probably was the result of their predaceous nature (attracting them to the carrier). Thus, showing a lack of discrimination, pseudoscorpions would grasp at passing arthropods as prey objects. If the arthropod was large, it would sometimes take

Table 2. Extant associations of arthropod phoresy involving pseudoscorpions. Abbreviations: EU = Europe; AS = Asia; NA = North America; CA = Central America; SA = South America; AU = Australia; NZ = New Zealand; AF = Africa, PA = Pacific Ocean. Families of pseudoscorpion genera listed: Chthoniidae (*Chthonius*, and *Lechytia*), Tridenchthoniidae (*Tridenchthonius*), Neobisiidae (*Neobisium*), Syarinidae (*Syarinus*), Cheiridiidae (*Apocheiridium, and Neocheiridium*), Sternophoridae (*Afrosternophorus*), Atemnidae (*Paratemnoides, Metatemnus, Oratemnus*, and *Titanatemnus*), Cheliferidae (*Chelifer, Ellingsenius, Lissochelifer, Mucrochelifer, Parachelifer*, and *Rhacochelifer*), Chernetidae (*Allochernes, Americhernes, Anthrenochernes, Chelodamus, Chernes, Cordylochernes, Dendrochernes, Dinocheirus, Hesperochernes, Incachernes, Lamprochernes, Lustrochernes, Muscichernes, Parachernes, Pselaphochernes, Semeiochernes, and Sphaenochernes*), and Withiidae (*Dolichowithius, Parawithius, Stenowithius, and Withius*).

| Carrier | Pseudoscorpion | Region | References |
|---|---|---|---|
| **ARACHNIDA** | | | |
| ARANEAE | | | |
| Heteropodidae | | | |
| *Delena cancerides* | *Afrosternophorus anabates* Harvey | AU | Harvey (1985) |
| *Olios fasciculatus* | *Lustrochernes grossus* (Banks) | NA | Hoff & Jennings (1974) |
| OPILIONES | | | |
| Sclerosomatidae | | | |
| *Leiobunum blackwalli* | *Pselaphochernes dubius* (O.-P. Cambridge) | EU | Vachon (1947) |
| *Leiobunum rotundum* | *Pselaphochernes dubius* (O.-P. Cambridge) | EU | Vachon (1947) |
| *Nelima gothica* | *Lamprochernes nodosus* (Schrank) | EU | Sankey (1949) |
| Phalangiidae | | | |
| *Oligolophus meadii* | *Pselaphochernes dubius* (O.-P. Cambridge) | EU | Cloudsley-Thompson (1956) |
| *Opilio parietinus* | *Lamprochernes nodosus* (Schrank) | EU | Sankey (1949) |
| *Mitopus morio* | *Lamprochernes nodosus* (Schrank) | EU | Sankey (1949) |
| *Nelima sylvatica* | *Lamprochernes nodosus* (Schrank) | EU | Jones (1978) |
| *Phalangium opilio* | *Lamprochernes nodosus* (Schrank) | EU | Leydig (1867), Spicer (1867) |
| *Phalangium opilio* | *Chelifer cancroides* (Linnaeus) | EU | Spicer (1867) |
| **INSECTA** | | | |
| ODONATA | | | |
| Unknown | Unknown | NA | Dunkle (1984) |
| ORTHOPTERA | | | |
| Acrididae | | | |
| Unknown | *Lustrochernes concinnus* Hoff | SA | Hoff (1947) |
| Rhaphidophoridae | | | |
| *Troglophilus cavicola* | *Chernes cavicola* G. Joseph | EU | Joseph (1882) |
| HEMIPTERA | | | |
| Reduviidae | | | |
| *Khafra praedo* | *Titanatemnus coreophilus* Beier | AF | Beier (1948) |
| COLEOPTERA | | | |
| Cerambycidae | | | |
| *Acanthophorus* sp. | *Titanatemnus congicus* Beier | AF | Vachon (1950) |

Table 2. Continued.

| Carrier | Pseudoscorpion | Region | References |
|---|---|---|---|
| *Acrocinus longimanus* | *Cordylochernes* sp. | CA | Muchmore (1971) |
| *Acrocinus longimanus* | *Cordylochernes costaricensis* Beier | NA | Beier (1947) |
| *Acrocinus longimanus* | *Cordylochernes nigermanus* Hoff | CA | Hoff (1944) |
| *Acrocinus longimanus* | *Cordylochernes panamensis* Hoff | CA | Hoff (1944) |
| *Acrocinus longimanus* | *Cordylochernes scorpioides* (Linnaeus) | CA | Ellingsen (1913), Zeh & Zeh (1992a) |
| *Acrocinus longimanus* | *Cordylochernes scorpioides* (Linnaeus) | CA | Calvert & Calvert (1917) |
| *Acrocinus longimanus* | *Cordylochernes scorpioides* (Linnaeus) | SA | Ellingsen (1905) |
| *Acrocinus longimanus* | *Lustrochernes intermedius* (Balzan) | SA | Aguiar & Buhrnheim (1992a) |
| *Acrocinus longimanus* | *Lustrochernes* sp. | CA | Muchmore (1971) |
| *Acrocinus longimanus* | *Parachelifer hubbardi* (Banks) | NA | Beier (1948) |
| *Acrocinus longimanus* | *Parachelifer lativittatus* (J. C. Chamberlin) | SA | Aguiar & Buhrnheim (1992a) |
| *Asemem striatum* | *Dendrochernes cyrneus* (L. Koch) | EU | Beier (1929) |
| *Batocera celebiana* | *Lissochelifer superbus* (With) | AS | Beier (1948) |
| *Callidium variabile* | *Dendrochernes cyrneus* (L. Koch) | EU | Kew (1929) |
| *Coelodon servum* | *Titanatemnus kibwezianus* Beier | AF | Beier (1948) |
| *Ergates spiculatus* | *Parachelifer persimilis* (Banks) | NA | Muchmore (1971) |
| *Ergates spiculatus* | *Lustrochernes grossus* (Banks) | NA | Muchmore (1971) |
| *Macrodontia cervicornis* | *Cordylochernes scorpioides* (Linnaeus) | SA | Aguiar & Buhrnheim (1992a) |
| *Macrotoma natala* | *Titanatemnus equester* (With) | AF | Beier (1948) |
| *Phymatodes testaceus* | *Dendrochernes cyrneus* L. Koch | EU | Jones (1978) |
| *Stenodontes spinibarbis* | *Lechytia chthoniiformis* (Balzan) | SA | Aguiar & Buhrnheim (1992a) |
| *Stenodontes spinibarbis* | *Lustrochernes intermedius* (Balzan) | SA | Aguiar & Buhrnheim (1992a) |
| *Stenodontes spinibarbis* | *Neocheiridium corticum* (Balzan) | SA | Aguiar & Buhrnheim (1991) |
| *Tragocephala* sp. | *Paratemnoides pallidus* (Balzan) | AF | Beier (1948) |
| *Tragosoma depsarius* | *Parachelifer persimilis* (Banks) | NA | Muchmore (1971) |
| Unknown | *Dendrochernes instabilis* (J. C. Chamberlin) | NA | Chamberlin (1934) |
| Unknown | *Lissochelifer* sp. | AS | Beier (1948) |
| Unknown | *Lustrochernes* sp. | NA | Muchmore (1971) |
| Unknown | *Metatemnus superior* Muchmore | AS | Muchmore (1972) |
| Unknown | Unknown | NA | Anonymous (1986) |
| Cicindelidae | | | |
| *Cicindela hirticollis* | *Parachelifer longipalpus* Hoff | NA | Muchmore (1971) |
| Cleridae | | | |
| *Thanasimus formicarius* | *Lamprochernes nodosus* (Schrank) | EU | Trappen (1906) |
| Coccinellidae | | | |
| *Chilocorus* sp. | *Oratemnus brevidigitatus* Beier | AF | Beier (1940) |
| Curculionidae | | | |
| *Rhynchophorus palmarum* | *Lustrochernes argentinus* (Thorell) | SA | Beier (1948) |
| Elateridae | | | |

Table 2. Continued.

| Carrier | Pseudoscorpion | Region | References |
|---|---|---|---|
| *Alaus oculatus* | *Americhernes oblongus* (Say) | NA | Leidy (1877) |
| *Alaus maculatus* | *Americhernes oblongus* (Say) | NA | Hagen (1879) |
| *Chalcolepidius rugatus* | *Parachernes nigrimanus* Beier | CA | Beier (1948) |
| *Chalcolepidius rugatus* | *Parachernes setosus* Beier | CA | Beier (1948) |
| *Pyrophorus phosphoreus* | *Lustrochernes argentinus* (Thorell) | SA | Beier (1948) |
| Lampyridae | | | |
| *Photuris* sp. | *Paratemnoides elongatus* (Banks) | NA | Lloyd *et al.* (1974), Lloyd & Muchmore (1975) |
| Passalidae | | | |
| *Passalus abortivus* | *Lustrochernes* aff. *reimoseri* Beier | SA | Aguiar & Buhrnheim (1992b) |
| *Passalus* aff. *coarctatus* | *Lustrochernes* aff. *reimoseri* Beier | SA | Aguiar & Buhrnheim (1992b) |
| *Passalus convexus* | *Americhernes* aff. *incertus* Mahnert | SA | Aguiar & Buhrnheim (1992b) |
| *Passalus convexus* | *Lustrochernes* aff. *reimoseri* Beier | SA | Aguiar & Buhrnheim (1992b) |
| *Passalus convexus* | *Tridenchthonius mexicanus* J. C. Chamberlin & R. V. Chamberlin | SA | Aguiar & Buhrnheim (1992b) |
| *Passalus elfriedae* | *Americhernes* aff. *incertus* Mahnert | SA | Aguiar & Buhrnheim (1992b) |
| *Passalus elfriedae* | *Lustrochernes* aff. *reimoseri* Beier | SA | Aguiar & Buhrnheim (1992b) |
| *Passalus elfriedae* | *Parawithius gracilimanus* Mahnert | SA | Aguiar & Buhrnheim (1992b) |
| *Passalus elfriedae* | *Tridenchthonius mexicanus* J. C. Chamberlin & R. V. Chamberlin | SA | Aguiar & Buhrnheim (1992b) |
| *Passalus interruptus* | *Lustrochernes* aff. *reimoseri* Beier | SA | Aguiar & Buhrnheim (1992b) |
| *Passalus interruptus* | *Parawithius gracilimanus* Mahnert | SA | Aguiar & Buhrnheim (1992b) |
| *Passalus interruptus* | *Tridenchthonius mexicanus* J. C. Chamberlin & R. V. Chamberlin | SA | Aguiar & Buhrnheim (1992b) |
| *Passalus interstitialis* | *Lustrochernes intermedius* (Balzan) | SA | Aguiar & Buhrnheim (1992b) |
| *Passalus interstitialis* | *Parawithius gracilimanus* Mahnert | SA | Aguiar & Buhrnheim (1992b) |
| *Passalus interstitialis* | *Tridenchthonius mexicanus* J. C. Chamberlin & R. V. Chamberlin | SA | Aguiar & Buhrnheim (1992b) |
| *Passalus latifrons* | *Lustrochernes* aff. *reimoseri* Beier | SA | Aguiar & Buhrnheim (1992b) |
| *Passalus latifrons* | *Tridenchthonius mexicanus* J. C. Chamberlin & R. V. Chamberlin | SA | Aguiar & Buhrnheim (1992b) |
| *Passalus punctiger* | *Lustrochernes argentinus* (Thorell) | SA | Beier (1948) |
| *Passalus rhodocanthopoides* | *Lustrochernes intermedius* (Balzan) | SA | Aguiar & Buhrnheim (1992b) |
| *Passalus rhodocanthopoides* | *Lustrochernes* aff. *reimoseri* Beier | SA | Aguiar & Buhrnheim (1992b) |
| *Passalus rhodocanthopoides* | *Parawithius gracilimanus* Mahnert | SA | Aguiar & Buhrnheim (1992b) |
| *Passalus rhodocanthopoides* | *Tridenchthonius mexicanus* J. C. Chamberlin & R. V. Chamberlin | SA | Aguiar & Buhrnheim (1992b) |
| *Passalus unicornis* | *Americhernes* aff. *incertus* Mahnert | SA | Aguiar & Buhrnheim (1992b) |
| *Passalus unicornis* | *Lustrochernes* aff. *reimoseri* Beier | SA | Aguiar & Buhrnheim (1992b) |

Table 2. Continued.

| Carrier | Pseudoscorpion | Region | References |
|---|---|---|---|
| *Passalus unicornis* | *Parawithius gracilimanus* Mahnert | SA | Aguiar & Buhrnheim (1992b) |
| *Passalus unicornis* | *Tridenchthonius mexicanus* J. C. Chamberlin et R. V. Chamberlin | SA | Aguiar & Buhrnheim (1992b) |
| *Passalus variiphyllus* | *Lustrochernes* aff. *reimoseri* Beier | SA | Aguiar & Buhrnheim (1992b) |
| *Venturius platyrhynus* | *Lustrochernes* aff. *reimoseri* Beier | SA | Aguiar & Buhrnheim (1992b |
| *Venturius transversus* | *Lustrochernes* aff. *reimoseri* Beier | SA | Aguiar & Buhrnheim (1992b) |
| *Venturius transversus* | *Tridenchthonius mexicanus* J. C. Chamberlin et R. V. Chamberlin | SA | Aguiar & Buhrnheim (1992b) |
| Platypodidae | | | |
| *Platypus* sp. | *Dolichowithius mediofasciatus* Mahnert | SA | Aguiar *et al.* (1992) |
| Unknown | Unknown | CA | Poinar (unpublished observation) |
| Prostomidae | | | |
| *Prostomis mandibularis* | *Lechytia* sp. | NA | Muchmore (1971) |
| Staphylinidae | | | |
| *Staphylinus fulvomaculatus* | *Incachernes mexicanus* Beier | NA | Beier (1933) |
| Unknown | *Dendrochernes instabilis* (J. C. Chamberlin) | CA | Muchmore (1971) |
| Unknown | *Dendrochernes cyrneus* (L. Koch) | EU | Lohmander (1939)c |
| Diptera | | | |
| Anthomyiidae | | | |
| *Anthomyia* sp. | *Lamprochernes nodosus* (Schrank) | EU | Gerstäcker (1859) |
| *Hylemyia floralis* | *Allochernes peregrinus* Lohmander | EU | Lohmander (1939) |
| *Ophyra leucostoma* | *Lamprochernes nodosus* (Schrank) | EU | Graham-Smith (1916) |
| *Pegomya affinis* | *Pselaphochernes scorpioides* (Hermann) | NA | Muchmore (1971) |
| *Pegomya apicalis* | *Hesperochernes* sp. | NA | Muchmore (1971) |
| *Pegomya apicalis* | *Lamprochernes savignyi* (E. Simon) | AF | Beier (1948) |
| *Pegomya apicalis* | *Lamprochernes savigyi* (E. Simon) | EU | Beier (1948) |
| Calliphoridae | | | |
| *Calliphora erythrocephala* | *Lamprochernes nodosus* (Schrank) | EU | Leydig (1867) |
| *Calliphora vomitoria* | *Lamprochernes nodosus* (Schrank) | EU | Donovan (1797) |
| *Calliphora vomitoria* | *Chelifer cancroides* (Linnaeus) | EU | Donovan (1797) |
| *Calliphora* sp. | Suborder *Cheliferinea* | SA | Berg (1893) |
| *Lucilia caesar* | *Lamprochernes nodosus* (Schrank) | EU | Masan & Kristofik (1992) |
| *Lucilia* sp. | *Lustrochernes argentinus* (Thorell) | SA | Beier (1948) |
| Culicidae | | | |
| *Aedes sticticus* | *Lamprochernes nodosus* (Schrank) | EU | Minar (1966) |
| Drosophilidae | | | |
| *Drosophila funebris* | *Lamprochernes nodosus* (Schrank) | EU | Vachon (1940, 1954a) |
| Heleomyzidae | | | |

Table 2. Continued.

| Carrier | Pseudoscorpion | Region | References |
|---|---|---|---|
| *Amoebalaria deffesa* | *Chelodamus* sp. | NA | Muchmore (1971) |
| *Amoebalaria* sp. | *Hesperochernes tamiae* Beier | NA | Muchmore (1971) |
| *Tephrochlamis canescens* | *Lamprochernes nodosus* (Schrank) | EU | Burr (1919) |
| Lonchaeidae | | | |
| *Lonchaea chorea* | *Lamprochernes nodosus* (Schrank) | EU | Jones (1978) |
| *Lonchaea chorea* | *Lamprochernes scorpioides* (Hermann) | EU | Jones (1978) |
| *Lonchaea laticonis* | *Rhacochelifer similis* Beier | AF | Vachon (1940) |
| *Lonchaea vaginalis* | *Lamprochernes nodosus* (Schrank) | EU | Graham-Smith (1916) |
| *Lonchaea* sp. | *Lamprochernes savignyi* (E. Simon) | EU | Jones (1978) |
| Muscidae | | | |
| *Fannia canalicularis* | *Lamprochernes nodosus* (Schrank) | EU | Macrae (1869), Zielke (1969) |
| *Hydrotaea similis* | *Lamprochernes nodosus* (Schrank) | EU | Masan & Kristofik (1992) |
| *Musca autumnalis* | *Lamprochernes nodosus* (Schrank) | EU | Jones (1970, 1978) |
| *Musca corvina* | *Lamprochernes nodosus* (Schrank) | EU | Graham-Smith (1916) |
| *Musca domestica* | *Chelifer cancroides* (Linnaeus) | EU | Nonidez (1917) |
| *Musca domestica* | *Chernes sanborni* Hagen | NA | Webster (1897) |
| *Musca domestica* | *Dinocheirus panzeri* (C. L. Koch) | EU | Preudhomme (1873) |
| *Musca domestica* | *Lamprochernes nodosus* (Schrank) | EU | Poda (1761), Carl (1994) |
| *Musca domestica* | *Neobisium sylvaticum* (C. L. Koch) | EU | PRESENT STUDY |
| *Musca domestica* | *Pselaphochernes scorpioides* (Hermann) | EU | Jones (1978) |
| *Musca domestica* | *Lamprochernes* sp. | NA | Muchmore (1971) |
| *Musca meteorica* | *Lamprochernes nodosus* (Schrank) | EU | Beier (1948) |
| *Musca meteorica* | *Chelifer cancroides* (Linnaeus) | EU | Beier (1948) |
| *Musca vicina* | *Muscichernes katoi* (Morikawa) | AS | Morikawa (1960) |
| *Musca* ? | *Pselaphochernes* sp. | NA | Muchmore (1971) |
| *Stomoxys calcitrans* | *Lamprochernes nodosus* (Schrank) | EU | Lukis (1831), Schiner (1872) |
| *Stomoxys calcitrans* | *Lamprochernes savignyi* (E. Simon) | EU | Jones (1978) |
| *Stomoxys* sp. | *Pselaphochernes scorpioides* (Hermann) | EU | Graham-Smith (1916) |
| Unknown | *Dinocheirus sicarius* J. C. Chamberlin | NA | Chamberlin (1952) |
| Neriidae | | | |
| *Odontolorozus longicornis* | *Dinocheirus arizonensis* (Banks) | NA | Zeh & Zeh (1992c) |
| Otitidae | | | |
| *Physiphora demandata* | *Lamprochernes nodosus* (Schrank) | EU | Clements (1987) |
| *Ulidia erythrophthalma* | *Lamprochernes nodosus* (Schrank) | EU | Low (1866) |
| *Ulidia erythrophthalma* | *Allochernes wideri* (C. L. Koch) | EU | Beier (1948) |
| Pantophthalmidae | | | |
| *Pantophthalmus tabaninus* | *Semeiochernes armiger* (Balzan) | CA | Zeh & Zeh (1992b) |
| Scenopinidae | | | |
| *Omphrale fenestralis* | *Lamprochernes nodosus* (Schrank) | EU | Vachon (1940) |

Table 2. Continued.

| Carrier | Pseudoscorpion | Region | References |
|---|---|---|---|
| Sphaeroceridae | | | |
| *Leptocera sylvatica* | *Pselaphochernes scorpioides* (Hermann) | EU | Cuthbertson (1982) |
| Unknown | *Pselaphochernes scorpioides* (Hermann) | EU | Weygoldt (1969) |
| Stratiomyidae | | | |
| *Hoplites bispinosus* | *Lamprochernes nodosus* (Schrank) | EU | Vachon (1940) |
| Syrphidae | | | |
| *Brachypalpus laphriformis* | *Lamprochernes nodosus* (Schrank) | EU | Gerstäcker (1859) |
| *Eristalis arbustorum* | *Lamprochernes nodosus* (Schrank) | EU | Jones (1978) |
| *Sargus iridatus* | *Lamprochernes nodosus* (Schrank) | EU | Jones (1978) |
| *Volucella zonaria* | *Lamprochernes nodosus* (Schrank) | EU | Berland (1932) |
| Tabanidae | | | |
| *Tabanus* sp. | Suborder Cheliferinea | SA | Berg (1893) |
| Unknown (Dexinae) | *Hesperochernes pallipes* (Banks) | NA | Banks (1895) |
| Unknown | *Parachernes argentatopunctatus* (Ellingsen) | SA | Beier (1948) |
| Unknown | *Lamprochernes savignyi* (E. Simon) | AU | Ellingsen (1913) |
| Tachinidae | | | |
| *Tachina larvarum* | *Lamprochernes nodosus* (Schrank) | EU | Beier (1948) |
| *Tachina larvarum* | *Chelifer cancroides* (Linnaeus) | EU | Beier (1948) |
| Tipulidae | | | |
| *Ctenophora pectinicornis* | *Anthrenochernes stellae* Lohmander | EU | Gardenfors & Wilander (1995) |
| *Ctenophora pectinicornis* | *Lamprochernes nodosus* (Schrank) | EU | Wagner (1892) |
| *Ctenophora pectinicornis* | *Chernes cimicoides* (Fabricius) | EU | Wagner (1892) |
| *Limonia decemmaculata* | *Pselaphochernes scorpioides* (Hermann) | EU | Jones (1978) |
| *Tipula unicincta* | *Syarinus obscurus* (Banks) | NA | Muchmore (1971) |
| *Tipula* sp. | *Syarinus obscurus* (Banks) | NA | Beier (1948) |
| *Zelandotipula* sp. | *Chernetidae* | SA | Matthiesen & Hahn (1981) |
| Unknown | "*Lamprochernes loewi* Hagen" (nomen nudum) | CA | Hagen (1879) |
| Unknown | *Lamprochernes savignyi* (Simon) | NZ | Muchmore (1971) |
| Unknown | *Lamprochernes nodosus* (Schrank) | AS | Redikorzev (1936) |
| Unknown | *Semeiochernes militaris* Beier | SA | Mahnert (1987) |
| Unknown | "Pseudoscorpionida" | PA (on boat) | Guilmette *et al.* (1970) |
| LEPIDOPTERA | | | |
| Arctiidae | | | |
| *Spilosoma rattrayi* | *Stenowithius bayoni* (Ellingsen) | AF | Beier (1932) |
| Cocytiidae | | | |
| *Cocytius duponchel* | *Neocheiridium triangulare* Mahnert et Aguiar | SA | Mahnert & Aguiar (1986) |
| Geometridae | | | |
| *Sterrha aversata* | *Rhacochelifer maculatus* (L. Koch) | EU | Vachon (1953) |

Table 2. Continued.

| Carrier | Pseudoscorpion | Region | References |
|---|---|---|---|
| Hesperidae | | | |
| *Pelopides tridens* | *Mucrochelifer bornoensis* (Ellingsen) | AS | Beier (1948) |
| Lymantriidae | | | |
| *Lymantria monacha* | *Chelifer cancroides* (Linnaeus) | EU | Ketterer (1955) |
| *Spilosoma rattsayi* | *Stenowithius bayoni* (Ellingsen) | AF | Beier (1932) |
| Noctuidae | | | |
| *Acronycta grisea* | *Apocheiridium* sp. | NA | Treat (1956) |
| *Acronycta morula* | *Apocheiridium* sp. | NA | Muchmore (1971) |
| *Acronycta ovata* | *Apocheiridium* sp. | NA | Treat (1956) |
| *Caenurgia crassiuscula* | *Dinocheirus pallidus* (Banks) | NA | Fenstermacher (1959) |
| *Catocala neogama* | *Apocheiridium* sp. | NA | Muchmore (1971) |
| *Rhyacia augur* | *Lamprochernes chyzeri* (Tömösvary) | EU | Vachon (1954) |
| Riodinidae | | | |
| *Eurybia* sp. | Unknown | CA | De Vries (personal communication) |
| *Synargus* sp. | Unknown | CA | De Vries (personal communication) |
| Unknown | *Withius piger* (Simon) | AF | Beier (1930) |
| Microlepidoptera | Unknown | EU | Berland (1932) |
| Hymenoptera | | | |
| Apidae | | | |
| *Apis mellifera* | *Chelifer cancroides* (Linnaeus) | NA | Filleul (1922) |
| *Apis mellifera* | *Ellingsenius fulleri* (Hewitt et Godfrey) | AF | Hewitt & Godfrey (1929) |
| *Apis mellifera* | *Ellingsenius hendrickxi* Vachon | AF | Vachon (1954) |
| *Apis mellifera* | *Ellingsenius sculpturatus* (Lewis) | AF | Ward (1887) |
| *Apis mellifera* | *Paratemnoides nidificator* (Balzan) | CA | Muchmore (1971) |
| Unknown | *Cordylochernes scorpioides* (Linnaeus) | SA | Tömösvary (1884) |
| "Wild bee" | *Lamprochernes* sp. | NA | Muchmore (1971) |
| Aulacidae | | | |
| *Pristaulacus niger* | *Dendrochernes* cf. *morosus* (Banks) | NA | Haack & Wilkinson (1986) |
| Formicidae | | | |
| *Acromyrmex lundi* | *Sphaenochernes bruchi* (Mello-Leitão) | SA | Mello-Leitão (1927) |
| *Oecophylla smaragdina* | Cheliferinea sp. | AS | Green (1908) |
| Ichneumonidae | | | |
| *Ephialtes mesocentrus* | *Chernes cimicoides* (Fabricius) | EU | Jones (1978) |
| Siricidae | | | |
| *Tremex columba* | *Dendrochernes* sp. | NA | Muchmore (1971) |

flight, carrying the pseudoscorpion along with it. Jones (1978) concurred and felt that phoretic behavior in pseudoscorpions was a modification of their original hunting instinct, which caused them to seize large animals that passed by.

We agree that phoresy in pseudoscorpions can be motivated by hunger, however not hunger for the carrier, but rather a desire to reach a new habitat that has a greater nutritional potential than the present location. Thus, in the great majority of, if not in all, cases involving arthropod phoresy in pseudoscorpions, the advantage and ultimate goal of the carrier is to reach a new habitat (i.e., dispersal). This is not to say that under other circumstances, the pseudoscorpion will not turn around and attack its potential carrier. An interesting case has been documented where a neriid fly, *Odontolorozus longicornis*, serves as both carrier and prey to *Dinocheirus arizonicus* (Zeh & Zeh 1992c). In this situation, the pseudoscorpion exhibited a clear distinction between phoretic and predatory behavior towards the fly. When initiating a phoretic relationship, the arachnid would grasp the fly's hind trochanter with its chela; when exhibiting predatory behavior, however, it would secure the fly with its pedipalpal chela in order to inject the victim with venom.

A difference between predatory and dispersal responses was demonstrated by Cuthbertson (1984) with a captured *Dendrochernes cyrneus*. When a female pseudoscorpion grasped a small piece of paper, as it would an arthropod appendage, it entered a quiescent state, which the author referred to as catalepsy. While in this state, any predatory activity was out of the question, showing that this type of grasping reflex was adapted for dispersal only. Additional observations on sex selection of carriers with *Semeiochernes armiger* also support the hypothesis that phoretic behavior is for dispersal only (Zeh & Zeh 1992b). The pseudoscorpions would only persist in grasping female timber flies (*Pantophthalmus tabaninus*), but quickly released their hold on enclosing males. This was considered an adaptation for dispersal, since only the female flies visit trees suitable for pseudoscorpion establishment. If phoresis in this association was initiated as a predatory response, then both sexes of the fly would be equally treated.

These reports demonstrate that the response of pseudoscorpions resulting in phoresis is quite separate from predatory actions and that phoretic behavior does not have predation as its basis.

That phoretic behavior between arthropods and pseudoscorpions can actually disperse the rider over long distances, even trans-oceanic, is suggested by the presence of *Ediogaryops pumilis* on Little Cayman Island in the Caribbean (Harvey 1985) and at least 11 species of 7 families on Krakatoa (Harvey 1986). In addition, pseudoscorpions have been found among airborne insect specimens collected over water on ships (Guilmette *et al.* 1970).

In both the extinct and extant examples of phoresy with platypodid beetles (see Tables 1 & 2), the pseudoscorpion probably fed upon mites, insect eggs, young larvae, and possibly nematodes that occured in the tunnels of the beetle (mites are also phoretic on platypodid beetles, but there are no reported examples of double phoresis involving mites and pseudoscorpions as in the harlequin beetle). That these phoretic associations may be highly specialized is shown by the constant presence of a specific pseudoscorpion on a particular host, undoubtedly related to the fact that both the carrier and pseudoscorpion occur in the same developmental habitat (soil, under bark, beetle galleries, rotting debris, etc.). This type of co-evolution probably developed over a period of time and was related to the survival strategy of the pseudoscorpion, which seems to gain most from

the association, since adaptations to survival in transitory habitats must be accompanied by effective dispersal mechanisms. Indirect benefits for the carrier could occur if it or its young fed on the developmental stages of the arachnid or if the pseudoscorpion fed on enemies of various stages of the carrier.

It is clear from Table 2 that most reported extant phoretic associations between pseudoscorpions and arthropods involve carriers in the Diptera. And most of these carriers have breeding stages in the soil, rotting debris, or wood galleries, habitats that would be attractive to pseudoscorpions. The next largest order of carriers belongs to representatives of the Coleoptera, with many of these beetles living in habitats similar to the fly carriers.

A concept in evolutionary biology which has been substantiated by a wide range of data is that of behavioral fixity (Boucot 1990). This maxim states that once a successful type of behavior has become established in an organism, it continues until the organism becomes extinct. It also implies that the behavior of extinct organisms will be similar to that of extant representatives in the same genus and often family. Representatives of all four families of pseudoscorpions mentioned in the present study as exhibiting phoresy in the fossil record have similar associations today with same groups of carriers. Even the method of attachment is similar in modern representatives to those of the fossils. For instance, in both the fossil and extant examples of pseudoscorpions carried by platypodid beetles, the pseudoscorpion holds on to an area under the posterior edge of the elytra with a single chela (compare Fig. 2 in the present study with fig. 1 of Aguiar *et al.* 1992). Thus, "modern" phoresy in pseudoscorpions has been in effect for at least 40 million years and probably much longer. Only one of the families of carriers in fossil associations (Braconidae) is not represented in reported extant associations. However, it is premature to say that the association is absent today: it probably has simply not yet been reported. The length of time that these associations have existed suggests that phoretic behavior may indeed be obligatory for the survival of certain species of pseudoscorpions, thus resulting in sophisticated capabilities of detection, attachment, and release regarding the carrier.

In the fossil example of platypodid carrier in Dominican amber (Fig. 2), the beetle is carrying phoretic nematodes as well as a pseudoscorpion. Microbivorous and phytophagous nematodes are often carried by arthropods in phoretic relationships, with the same advantages to the nematode as is obtained for phoretic pseudoscorpions, namely transportation to a new environmental with nourishment and breeding potential (Poinar 1983).

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